

THE NEWLY DISCOVERED MALE OF *AUSTROCONOPS*
(CERATOPOGONIDAE: DIPTERA) WITH A DISCUSSION
OF THE PHYLOGENY OF THE BASAL LINEAGES OF
THE CERATOPOGONIDAE

A. BORKENT, W. W. WIRTH, AND A. L. DYCE

(AB) Biosystematics Research Centre, Agriculture Canada, Ottawa, Ontario, K1A 0C6, Canada; (WWW) Systematic Entomology Laboratory, BBII, Agricultural Research Service, USDA, % National Museum of Natural History, NHB-168, Washington, D.C. 20560, U.S.A.; (ALD) % CSIRO, Division of Tropical Animal Science, Indooroopilly, Queensland, 4068, Australia.

Abstract.—The male of *Austroconops mcmillani* Wirth and Lee is described for the first time and the female redescribed. Character states of the head capsule, thorax, trochanter and terminalia suggest that *Austroconops mcmillani* is the sister group of Forcipomyiinae plus Dasyheleinae plus Ceratopogoninae. *Leptoconops* Skuse is hypothesized as the sister group of this entire assemblage. Alternatively, character states in the antenna and maxillary palpus may indicate that *Austroconops* Wirth and Lee and *Leptoconops* are sister groups. *Austroconops mcmillani* is placed in the new subfamily **Austroconopininae**.

When Wirth and Lee (1958) described *Austroconops mcmillani* as a new genus and species, they suggested that the species seemed closest to *Culicoides*. This was a position well within the Ceratopogonidae, but other character states indicated a relationship with *Leptoconops*, a genus at the very base of Ceratopogonidae phylogeny. At that time, only females were known. No further material was available until recently, when two of us (WWW, ALD) collected a small sample including both males and females in Western Australia. The recent discovery of the male of this species provided an exciting opportunity to reexamine the phylogenetic placement of *Austroconops*. In this paper we describe the male of *A. mcmillani* and discuss the phylogeny of the main lineages of the Ceratopogonidae. Our results show that *A. mcmillani* is an early lineage within the Ceratopogonidae and requires placement in

a new subfamily, which we name Austroconopininae.

MATERIALS AND METHODS

The three males and ten females that form the basis of this study were collected at Yankech National Park, Western Australia, Oct. 22–Nov. 1, 1985 between 0942–1645 h with a truck trap by WWW and ALD.

The specimens were first examined alive and then in alcohol. They were cleared in KOH, examined in glycerine, and finally mounted on microscope slides in Canada Balsam. They are now deposited in the United States National Museum, Washington, D.C. (one ♂, two ♀), Australian National Insect Collection, Canberra (one ♂, four ♀), Canadian National Collection, Ottawa (one ♂, two ♀), Western Australian Museum, Perth (one ♀), and the British Museum (Natural History), London (one ♀).

Terms used in this paper follow those of Downes and Wirth (1981). Terms for sensilla of the antennae follow those used by Wirth and Navai (1978). Some of the terms for the male terminalia used in this paper are new to ceratopogonid studies and are those tentatively proposed by Wood and Borkent (1982) for other members of the Culicomorpha.

The composition of subfamilies and tribes follows the classification used by Downes and Wirth (1981).

Our approach to character analysis and phylogenetic interpretation is essentially the cladistic methodology as outlined by Wiley (1981). Polarities of character states were determined by outgroup comparisons.

AUSTROCONOPINAE, NEW SUBFAMILY

Diagnosis.—Male flagellomere 13 with subbasal constriction; male and female with: four-segmented maxillary palpus with only one segment distal to the one bearing the sensory organs; anapleural suture well developed, extending to anterior margin of anepisternal cleft; posterior margin of scutellum forming nearly a 90° angle in dorsal view; well developed empodium on each leg; wing with two well developed radial cells.

The type genus of the subfamily is *Austroconops* Wirth and Lee.

DESCRIPTION OF *AUSTROCONOPS* *McMILLANI* WIRTH AND LEE

Male ($n = 3$) (Figs. 1A, B, 2B, 3A, C, 4A, B, D–G, 5C, D).—Small biting midge, wing 1.04–1.05 mm long; body jet black, antennae, legs dark brown, except for pale annulus near bases of all tibiae; wings dull milky white with anterior veins dark brown, media barely discernable (Fig. 4B).

Head: Antenna (Figs. 1B, 3C): scape large, lacking setae and ventral apodeme; pedicel with basal foramen large; 13 flagellomeres, measurements (in microns) as follows: 98, 31, 31, 31, 28, 28, 28, 25–28, 25–28, 28–31, 36, 92, 134; flagellomere 13 with sub-

basal constriction; plume well developed (Fig. 1B); 1st flagellomere with two sensory pits, one deeper than the other, each with numerous elongate, hyaline sensilla trichodea (Fig. 3A). Eyes pubescent, only slightly separated dorsomedially, frons with single median seta (Fig. 1A); postoccipital ridge well developed with posterior tentorial pits on ventral margin (Fig. 5D); clypeus wider than long (Fig. 1A); maxillary palpus with 4 segments, only 1 segment distal to segment bearing sensory organs; segment 3 with apical $\frac{2}{3}$ swollen, with patch of sensilla which are slightly bulbous apically and scattered amongst ridges from which spicules arise (Fig. 2B).

Thorax: Setae restricted to scutum and scutellum; scutum with dorsomedial and dorsolateral setae in single row (Fig. 4A), lacking anterior tubercle; transverse suture well developed laterally; anepisternal cleft well developed, rounded ventrally (Fig. 5C); anapleural suture well developed, extending to anterior margin of anepisternal cleft; from dorsal view, posterior margin of scutellum forming nearly a 90° angle (Fig. 4A).

Wing (Fig. 4B): Length 1.03–1.06 mm; costa extending 0.76–0.77 of wing length; radial veins, base of media and r-m darkly pigmented; r-m very oblique, forming almost a straight line with base of media and posterior side of radial cells; two broad radial cells present; media very faint in middle section of wing, where it forms a long petiole to medial fork, the fork a little posterior to level of cubital fork; cubitus very faint; anal angle broad, alula fringed, fringe of posterior wing margin a simple row of alternating long and short hairs; macrotrichia absent, microtrichia numerous, erect and imparting milky appearance to wing.

Legs: Moderately robust, unmodified, unarmed, with short setae; fore and mid trochanter lacking pair of thick setae; four spines present on apex of hind tibia, with elongate spicules in linear row just proximal to spines; fourth tarsomeres subcylindrical; fifth tarsomeres unarmed; claws small,

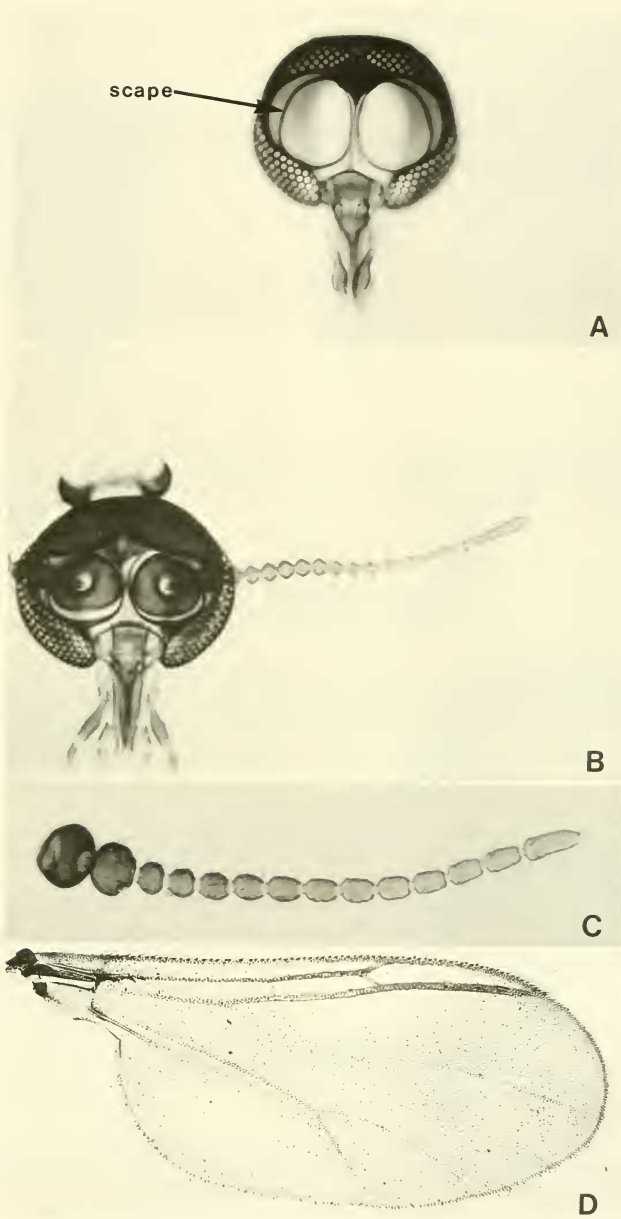


Fig. 1. Structures of *Austroconops mcmillani*. A, Anterior view of male head capsule. B, Male antenna. C, Female antenna. D, Female wing.

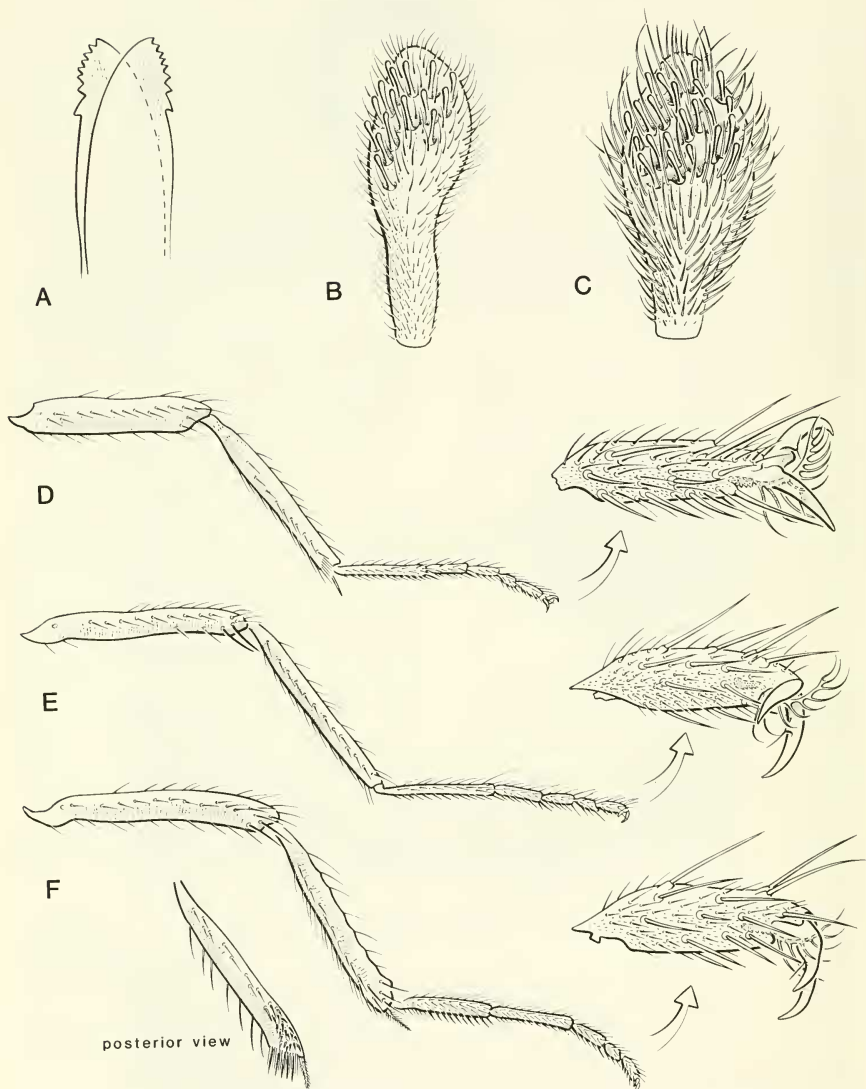


Fig. 2. Structures of *Austroconops mcmillani*. A, Female mandibles. B, Male third palpal segment. C, Female third palpal segment. D, Female foreleg and fifth tarsomere. E, Female midleg and fifth tarsomere. F, Female hindleg and fifth tarsomere.

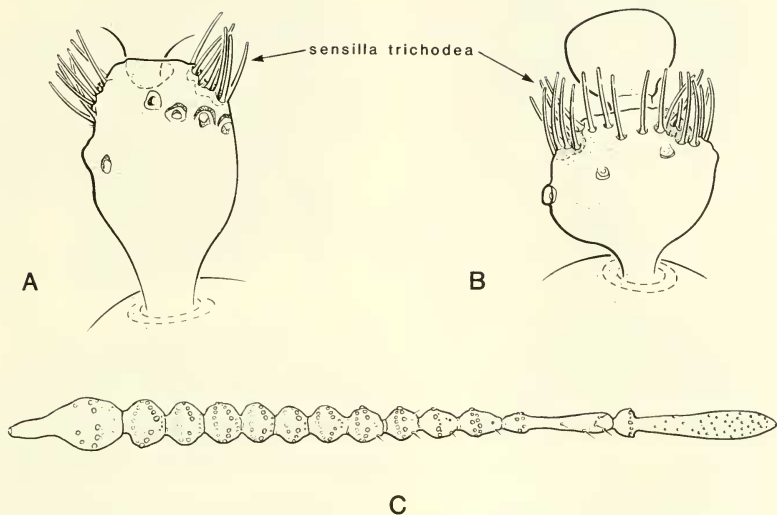


Fig. 3. Structures of *Austroconops mcmillani*. A, Male first flagellomere. B, Female first flagellomere. C, Male flagellum.

equal, each with very slender subbasal inner tooth, apex of each claw bifid; slender empodium present.

Terminalia (Fig. 4D–G): Tergite (tg) 9 slightly bilobed apically, some scattered setae on dorsal surface, row of setae on posterior margin; apicolateral processes absent; cerci well developed, located under ventral surface of tg 9; gonocoxite stout; gonostylus gradually tapering to pointed tip; parameres well developed, fused basally, bilobed apically; aedeagal sclerite with lateral tooth directed ventrally; ventral plate stout, compact, bilobed apically from dorsal view, laterally fused to base of gonocoxite; a single median setose lobe ventral to the median sclerite, with spicules.

Female (n = 10) (Figs. 1C, D, 2A, C–F, 3B, 4C, H).—As for male except as follows: antenna as in Fig. 1C; 13 flagellomeres, measurements (in microns) as follows: 48–50, 22–25, 25–28, 28, 25–28, 28–31, 28–31, 31–34, 28–34, 31–36, 34–36, 34–36, 48–56;

first flagellomere with two deeper sensory areas from which arise numerous, elongate, hyaline sensilla trichodea (Fig. 3B); clypeus with 6–8 setae; proboscis short; labrum with two pairs of small, stout sensilla apically; mandible with 7–8 distal teeth (Fig. 2A), fulcrum absent; lacinia with fine teeth; thorax as described for male; claws as for male but apex of each claw simple (Fig. 2D–F).

Wing (Figs. 1D, 4C): Length 0.88–0.93 mm; costa extending 0.87–0.90 of wing length; similar to male but broader.

Terminalia (Fig. 4H): Sternum (st 9) with posterior portion continuous medially and with either an anteriorly or posteriorly directed medial bend, depending on a more anterior or posterior angle of view (bend medially pale in some specimens); a pair of anteromedially directed apodemes arise from lateral arms of st 9; farther anteriorly an M shaped apodeme present, located ventral to common oviduct; 2 large, subequal, subspherical spermathecae, each with thick,

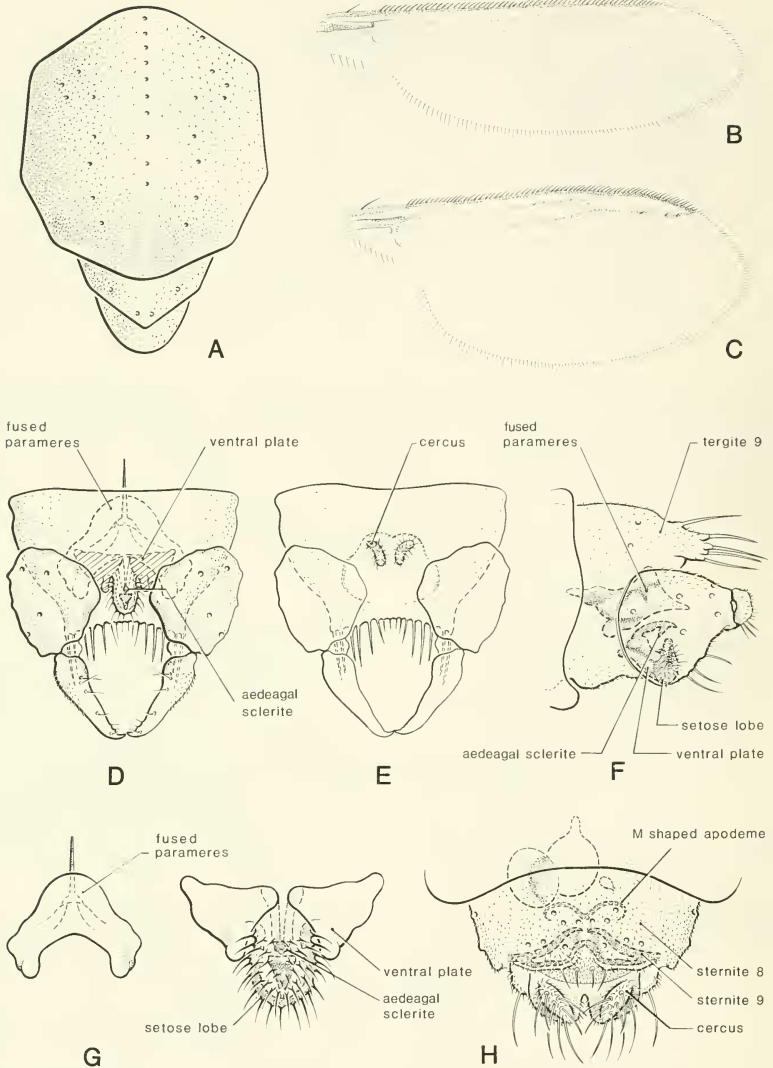
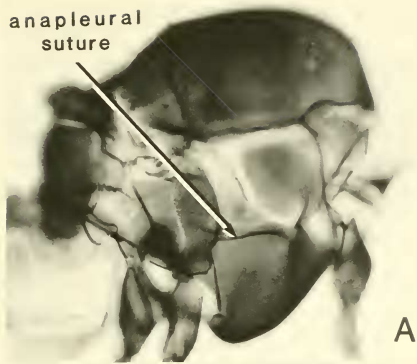
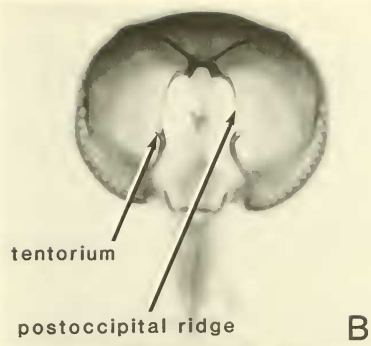


Fig. 4. Structures of *Austroconops mcmillani*. A, Dorsal view of male thorax. B, Male wing. C, Female wing. D, Ventral view of male terminalia. E, Ventral view of male terminalia with parameres and aedeagus removed. F, Lateral view of male terminalia. G, Details of parameres and aedeagus from ventral view. H, Ventral view of female terminalia.



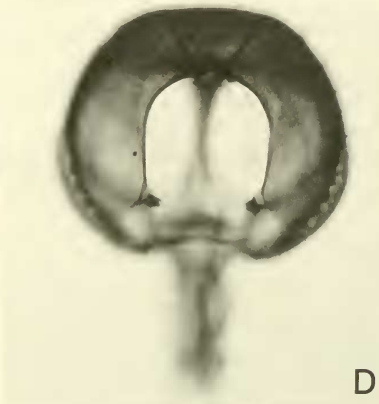
A



B



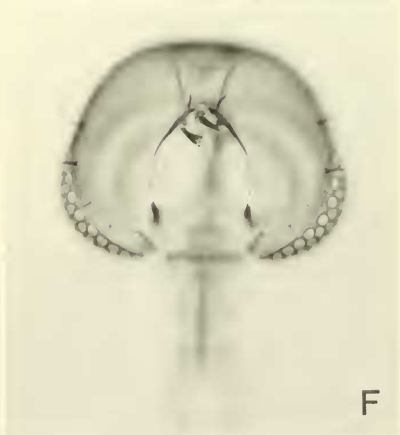
C



D



E



F

Fig. 5. Lateral view of thorax and posterior view of head capsule of males. A, B, *Leptoconops catawbae* (Boesel). C, D, *Austroconops mcmillani*. E, F, *Culicoides spinosus* Root and Hoffman.

pigmented neck, and a very small, oval, vestigial spermatheca present.

Distribution.—*A. mcmillani* is known only from Western Australia (Fig. 6). These are localities from Wirth and Lee (1958), our new collection and from a specimen collected by Don Colless at Augusta, Oct. 3, 1970 (ANIC). The record by Wirth and Lee (1958) from Darban is actually from Darkan.

Bionomics.—Wirth and Lee (1958) recorded females of this species biting the eyelids of man.

When we observed live and freshly killed males and females, the body fluids showed a distinct blue-green coloration. It may indicate a larval habitat abundant with algal growth which was observed commonly in damp areas of exposed limestone at Yan-chep. After preservation in 70% ethyl alcohol this coloration was lost within a few days.

Recognition.—Male and female *Austroconops* can be recognized using the key of Wirth et al. (1974) with the following modifications. Couplet 6 "Claws of both sexes small, equal and simple" should be changed to "Claws of both sexes small, equal and simple or with slender basal tooth"; couplet 6 "empodium small or rudimentary" should be changed to "empodium rudimentary to well developed"; from couplet 11 "antenna without minute sensory pits ringed with fine setae" should be deleted.

DISCUSSION OF CHARACTER STATES

CLADISTIC RELATIONSHIPS OF BASAL LINEAGES

In this section we discuss the characters that we recognize as important in determining the relationships between the basal lineages of the Ceratopogonidae. To provide a cladistic basis to the analysis, we compared character states within the family to those of all other Culicomorpha families. We paid closest attention to the Chiron-

omidae as the sister group of Ceratopogonidae (Hennig, 1973; Wood and Borkent, in press). Within the Ceratopogonidae we examined nearly every genus on a worldwide basis and, within *Leptoconops*, *Dasyhelea*, Forcipomyiinae, and many genera of Ceratopogoninae, we examined virtually all Nearctic species and many outside of this region.

The numbering of characters listed below refers to the numbers presented on the concluding cladogram (Fig. 8C).

Some workers (e.g. Krivosheina, 1962; Zilahi-Sebess, 1960) have questioned the phylogenetic position of *Leptoconops* but we consider the evidence presented below (characters 1 and 2) to be sufficient evidence to include this genus in the Ceratopogonidae. As far as we know, there is no evidence that contradicts that conclusion.

1.—Genital fork (sternite 9) of female genitalia well developed, with vaginal apodeme extending along dorsal wall of common oviduct (plesiomorphic); vaginal apodeme very reduced or absent (apomorphic).

Saether (1977) suggested that the absence of the vaginal apodeme (his notum) was a synapomorphy of the Ceratopogonidae and we agree. All Chironomidae, Simuliidae, and Thaumaleidae have a well developed vaginal apodeme. Some *Dasyhelea* have anterior projections from sternite 9 but we consider these secondarily derived and only superficially similar to the vaginal apodeme of the outgroup.

All Culicoidea lack a vaginal apodeme, indicating that the loss is susceptible to homoplasy.

2.—Larval pharyngeal apparatus present and acting as a sieve or absent; not acting as a crushing structure (plesiomorphic); pharyngeal apparatus a grinding and sifting structure (apomorphic).

All known larvae of Ceratopogonidae have a characteristic, well developed pharyngeal complex consisting of two strongly diverging dorsal arms and a series of combs

serving to grind and sort food (Clastrier, 1971; Lawson, 1951; Nielsen, 1951; Saunders, 1924). This unique modification of the pharyngeal filter is evidence for the monophyly of the family, including the genus *Leptoconops*. Wood and Borkent (in press) considered the pharyngeal filter as the ancestral condition in the Culicomorpha; it is found in Dixidae and Culicidae of the Culicoidea, and in the Thaumaleidae of the Chironomoidea. They regarded the ceratopogonid pharyngeal apparatus as a synapomorphy of the family. When the larva of *Austroconops* is found, we predict that it, too, will have a pharyngeal apparatus like other ceratopogonids.

We know of no Culicomorpha larva with an apparatus similar to that of ceratopogonids. Although the larva of the chironomid *Archaeochlus* has a strongly reinforced U shaped strut supporting the opening of the pharynx (pers. obs.), it has none of the specialized modifications of the ceratopogonid pharyngeal apparatus. The larva of *Bittacomorpha* Westwood (Ptychopteridae) has a pharyngeal structure which looks superficially similar to that of ceratopogonids (pers. obs.) but we do not consider it a homologous character state. The larva of *Ptychoptera* Meigen has a pharyngeal filter of the type found in Culicidae and many other families of Nematocera.

Further morphological studies are needed to determine homologies between nematoceran families.

3.—Setae on vertex scattered or in dorsolateral arrangement (plesiomorphic); in addition to other setae on vertex, a single seta located medially on frons just dorsal to where eyes meet (apomorphic).

The apomorphic character state is unique within the Culicomorpha and probably within the Diptera. We presently interpret the apomorphic state as a synapomorphy of Ceratopogonidae excluding Leptoconopinæ. Female *Leptoconops* lack the bristle. However, males have a dark protuberance

in this area and we are unsure as to whether it is a seta in modified form. Hence, the apomorphic state might in fact be a synapomorphy of all Ceratopogonidae.

Some *Forcipomyia* species have so many setae on the vertex and frons that it is sometimes difficult to pick out the single seta. However, careful study indicates that it is present in these species also.

4.—Postoccipital ridge poorly sclerotized and tentorium directed in an anteroventral-posterodorsal angle (plesiomorphic); postoccipital ridge well developed and tentorium at a horizontal plane (apomorphic) (Fig. 5B, D, F).

The plesiomorphic condition is found in all species of *Leptoconops* and Chironomidae. The postoccipital ridge of all other Ceratopogonidae is well developed and their tentorium is on a horizontal plane.

We have presented what may in fact be two characters as only one. The strengthening of the postoccipital ridge may be directly related to the more ventral position of posterior tentorial pit.

5.—Larva with three thoracic and nine (or 10) abdominal segments (plesiomorphic); larva with body segments secondarily divided (apomorphic).

The secondarily divided body segments of *Leptoconops* are unique within the Culicomorpha.

6.—Anapleural suture well developed, extending to anterior margin of anepisternal cleft (plesiomorphic); anapleural suture short, extending to posterior margin of anepisternal cleft (apomorphic) (Fig. 5A, C, E).

The plesiomorphic character state is present in nearly all chironomids, *Leptoconops* and *Austroconops*. All other ceratopogonids exhibit the apomorphic state.

7.—Trochanter of fore and midleg with only thin, simple setae (plesiomorphic); trochanter of fore and midleg each with pair of thick, contiguous setae (apomorphic) (Fig. 7A, B).

The apomorphic state is unique within the Diptera. In the *Leptoconops* species we examined there was either a single or pair of minute setae in a shallow pit in this same area. These may be homologous to those setae in the apomorphic state.

Two instances of further modifications were found within the group defined by the synapomorphy. Both occur in the subfamily Ceratopogoninae. Female *Sphaeromias longipennis* (Loew) have 3 thick setae on the midleg and *Probezzia atriventris* Wirth have 4. Other species of *Probezzia* Kieffer examined (6 Nearctic species) have only two.

8.—Posterior margin of scutellum rounded in dorsal view (plesiomorphic); posterior margin forming nearly a 90° angle (apomorphic) (Fig. 4A).

The apomorphic state is unique within Ceratopogonidae and Chironomidae. Representatives of Thaumaleidae and at least some Simuliidae have an angular scutellum but this is interpreted here as homoplasy. All examined Culicoidea have a rounded scutellum.

9.—Larval thoracic and abdominal setae arising from more or less flat areas of cuticle (plesiomorphic); setae arising from cuticular projections (apomorphic).

The apomorphic condition is unique within the Culicomorpha.

10.—Male flagellomeres lacking longitudinal striations (plesiomorphic); flagellomeres with longitudinal striations (apomorphic).

The apomorphic condition is unique within at least the Culicomorpha.

11.—Male and female scape lacking ventral apodeme (plesiomorphic); scape with ventral apodeme (apomorphic).

The apomorphic condition is unique within the Diptera. The ventral apodeme abuts laterally against a dorsal apodeme arising from the tentorium near the anterior tentorial pit. The apodeme appears to act as a "stop" to prevent rotation, at least in one direction, of the scape.

12.—Sternite 9 of female terminalia

forming a continuous band ventrally (plesiomorphic); sternite 9 discontinuous medially, forming two halves (apomorphic) (Fig. 8B).

The apomorphic condition is unique within the Diptera. Chironomidae, Simuliidae, and Thaumaleidae all have a well developed, sclerotized, continuous sternite 9. In the Culicoidea only a weak sternite 9 is present (Harbach and Knight, 1980, as upper vaginal lip). All members of the Ceratopogoninae have a discontinuous sternite 9.

The above proposed synapomorphies form a nested set as illustrated in the cladogram presented in Fig. 8C. Leptoconopinae is recognized as the sister group of all other Ceratopogonidae. *Austroconops* is the sister group of the Forcipomyiinae plus *Dasyheleinae* plus Ceratopogoninae.

ALTERNATE HYPOTHESIS

In this section we discuss those character states which may suggest a sister group relationship between *Austroconops* and *Leptoconops*. Although we currently consider these characters to be homoplastic, future work may support the interpretation of these as true synapomorphies.

Shape of basal foramen of pedicel.—In both *Leptoconops* and *Austroconops* the pedicel has a very large basal foramen (Figs. 1B, 8A). In *Dasyhelea* and Forcipomyiinae it is somewhat smaller and in Ceratopogoninae there is only a small foramen. Outgroup comparisons show that all Chironomoidea and most Culicoidea have a small foramen (*Chaoborus* Lichtenstein has a wide foramen), suggesting that the very wide foramen in *Leptoconops* and *Austroconops* could be a synapomorphy. However the presence of an intermediate condition in *Dasyheleinae* and Forcipomyiinae suggests that the wide foramen may be plesiomorphic within the Ceratopogonidae.

If taken as a valid indicator of relationship, *Leptoconops* and *Austroconops* would be regarded as sister groups and these two

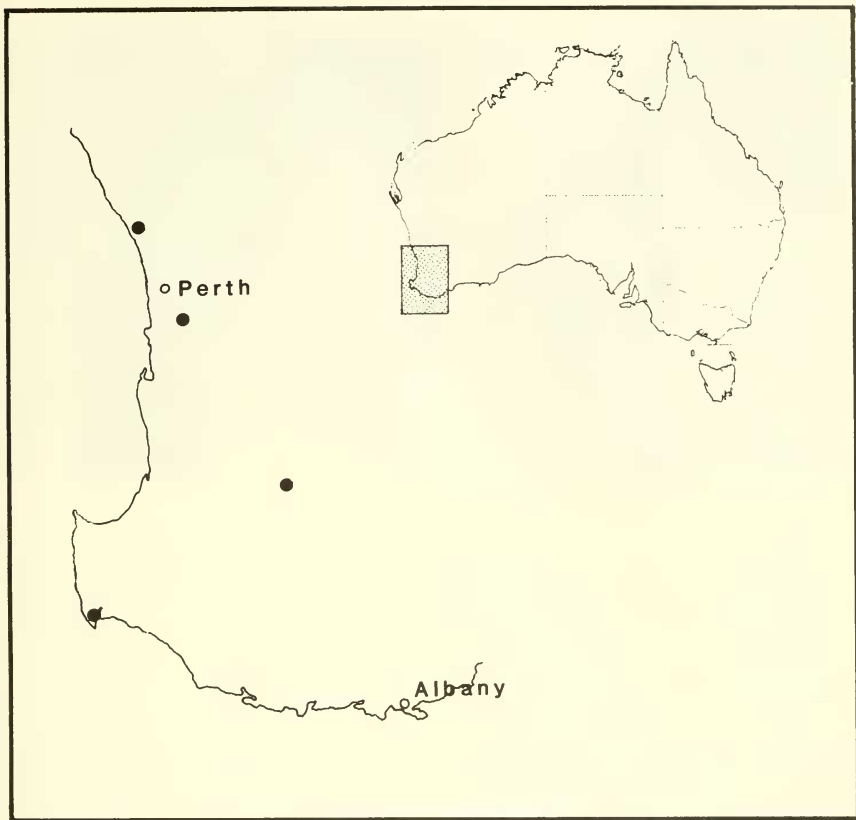


Fig. 6. Distribution of *Austroconops mcmillani*.

genera, together with Dasyheleinae and Forcipomyiinae would be recognized as a monophyletic unit. Characters 3, 4, 6 and 7 would be hypothesized as having evolved at least twice. We consider that unlikely.

Subbasal constriction of male flagellomere 13.—Both *Leptoconops* and *Austroconops* exhibit this feature. All other Ceratopogonidae have a more or less cylindrical or somewhat swollen 13th flagellomere. Outgroup comparisons show that the feature is unique within the Chironomoidea but that within the Culicoidea, a similar condition

appears in the Chaoboridae and some Culicidae. Although the character state is susceptible to homoplasy, these data suggest that a subbasal constriction is a synapomorphy of *Leptoconops* and *Austroconops*. If this character state is a good synapomorphy, characters 3 and 4 would have evolved at least twice.

Number of palpal segments.—Both *Leptoconops* and *Austroconops* have only four palpal segments with only one apparent segment distal to segment 3 which bears the sensilla. All other families in the Culico-

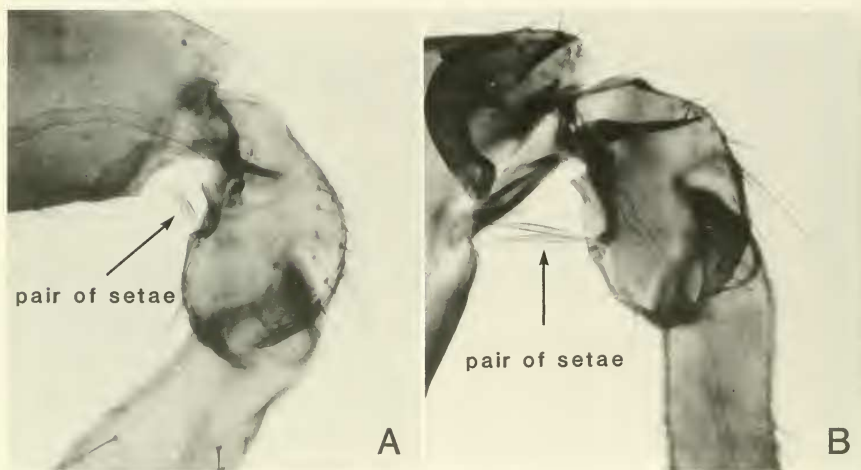


Fig. 7. Trochanter of *Mallochohelea atripes* Wirth. A, Foreleg. B, Midleg.

morpha have five palpal segments with only a few representatives of Chironomidae and Culicidae having a reduced number. Nearly all other ceratopogonids have five segments. Instances of a lower number in some ceratopogonids are almost certainly not homologous to that of either *Austroconops* or *Leptoconops* (*Paradasyhelea* Macfie, a few species of *Culicoides*, *Baeohelea* Wirth and Blanton, *Nannohelea* Grogan and Wirth, *Camptopterohelea* Wirth and Hubert, *Fittkauhelea* Wirth and Blanton, *Diaphanobezzia* Ingram and Macfie, *Parastilobezzia* Wirth and Blanton, *Leptohelea* Wirth and Blanton, *Baeadasymyia* Clastrier and Raccurt, *Parabezzia* Malloch, *Nilobezzia* Kieffer).

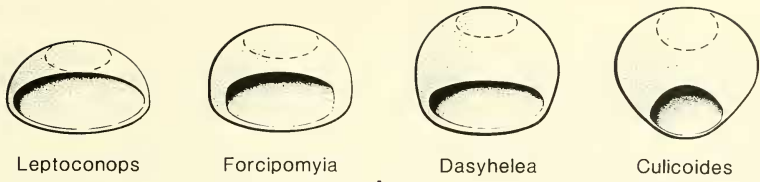
Although nearly all the ceratopogonid genera noted above have a reduced number of palpal segments, the palpi of almost all look quite different from *Austroconops* and *Leptoconops*. Only in *Parabezzia* and *Fittkauhelea*, which are probably closely related to each other, are there four palpal segments with only one segment distal to the sensilla bearing segment (segment 3). This indicates that the character state is susceptible to ho-

moplasia. However, because *Parabezzia* and *Fittkauhelea* are almost certainly quite distantly related to *Austroconops* and *Leptoconops*, the state in *Leptoconops* and *Austroconops* may yet be a synapomorphy.

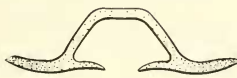
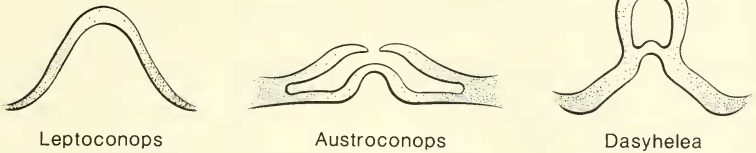
OTHER CHARACTER STATES

In this section we discuss character states which either conflict with our interpretation of the character states given above, character states that are not of use phylogenetically but which have misled some workers, and those that may be useful in the future but which cannot now be interpreted because of unsure homologies. In particular we discuss each character discussed by previous authors who have dealt with *Austroconops* or the relationships between the major lineages of Ceratopogonidae.

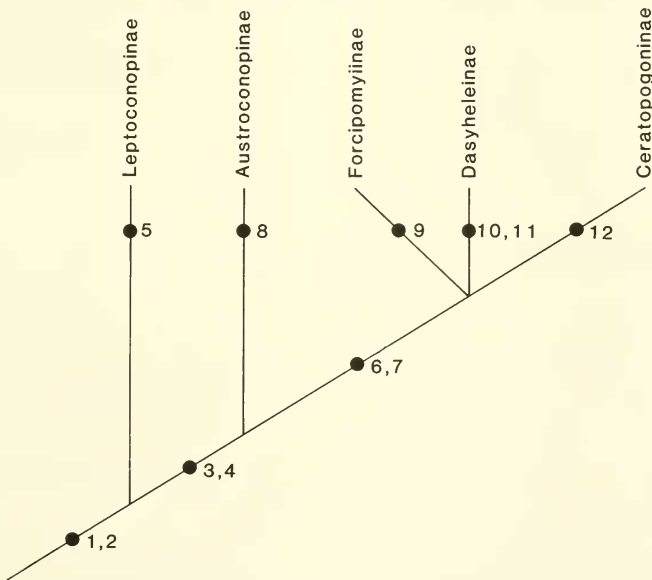
Wirth and Lee (1958), when they first described *Austroconops*, noted that some character states indicated relationship with *Culicoides* while others suggested connections with *Leptoconops*. Characters shared with *Culicoides* or other members of the Ceratopogoninae were: similarities in wing venation, absence of wing macrotrichia, pres-



A



B



C

Fig. 8. A, Oblique lateral view of pedicels of four male ceratopogonids. B, Sternite 9 of various female ceratopogonids (diagrammatic). C, Phylogeny of the basal lineages of Ceratopogonidae; numbers refer to apomorphic character states in the text.

ence of humeral pits, no antennal sculpturing and small, equal claws without empodium. Character states shared with *Leptoconops* were: shape of maxillary palpus, absence of macrotrichia, presence of humeral pits, two large and one minute spermathecae, and vestigial empodium. Some of these characters are discussed in the preceding sections.

Boorman and Lane (1979) also discussed the phylogenetic placement of *Austroconops*. They suggested that the similarities between Culicoidini and *Austroconops* were convergent and that *Austroconops* was a member of the Ceratopogonini. The character states they discussed were not interpreted cladistically and did not include the possibility noted by Wirth and Lee (1958) of a relationship with *Leptoconops*.

Some of the character states discussed by Boorman and Lane (1979) are analyzed above. Others are in the following section.

Our results also bear on the conclusions of Remm's (1975) cladistic study of the various genera of Ceratopogonidae. Remm did not discuss outgroup character states and therefore may have misinterpreted the polarity of several of these. He concluded that his Forcipomyiinae (including *Forcipomyia*, *Atrichopogon* and *Dasyhelea*) was the sister group of his Ceratopogoninae (including Stilobezziini, Ceratopogononini and *Culicoides*) on the basis of four synapomorphies that are included in the following discussion of characters. These two subfamilies were considered the sister group of his Palpomyiinae.

Sensilla on 1st flagellomere.—One or more sensilla coeloconica are present on the first flagellomere of females of *Leptoconops*, Culicoidini and many Ceratopogonini. In *Leptoconops* they are of the sensilla ampullacea type. In *Austroconops* they are represented by two depressed areas with clumps of long, slender sensilla trichodea. Sensilla coeloconica are also present in the same position in the chironomid *Archaeocheilus bicirratus* Brundin, which belongs to the only

known genus in that family with biting mouthparts (other species in the genus were not examined for antennal sensilla). This character state distribution indicates that the presence of sensilla coeloconica is plesiomorphic within the Ceratopogonidae and that they have probably been lost several times within the family.

The sensilla of *Leptoconops* have been previously overlooked or described only as erect pores or campaniform sensilla (e.g. Clastrier and Wirth, 1978). In fact, these pores lead to interior pockets which have well developed sensilla coeloconica called ampullacea. The sunken position of these sensilla may be a synapomorphy of *Leptoconops* but we are not sure that they occur in all species.

Number of flagellomeres of female.—*Leptoconops* females are unique within Ceratopogonidae in possessing 11–12 flagellomeres. All other ceratopogonids have 13, with rare exceptions (e.g. some species of *Brachypogon* Kieffer). Outgroup comparisons make the character states difficult to interpret. Chironomidae have 5–14, Simuliidae have 7–9, Thaumaleidae have 10, Dixidae have 14, and Chaoboridae and Culicidae all have 13.

Antennal sculpturing.—See discussion under character 9 above.

Mandible shape.—Contrary to the suggestion by Boorman and Lane (1979) that the "pointed and roughly serrated" mandibles of *Austroconops* are typical of the "higher Ceratopogonidae," we see no shared derived character states of the mandible of *Austroconops* with those of *Leptoconops*, *Culicoides*, those members of Ceratopogoninae with biting mouthparts (some are reduced), or other biting members of the Culicomorpha.

Previous reports show that all ceratopogonids with biting mouthparts possess a fulcrum about halfway down the length of the mandible (Gad, 1951). The fulcrum is also present in *Leptoconops* (pers. obs.). This mechanism allows the mandibles to artic-

ulate against one another and produce the outwardly directed cutting motion to allow feeding. *Austroconops mcmillani* is unique amongst the biting members of the Ceratopogonidae in lacking the mandibular fulcrum. This is probably an autapomorphy, as the fulcrum is also present in Simuliidae (Wenk, 1962). However, examination of *Archaeochlus bicirratu*s (Chironomidae) failed to provide evidence of a fulcrum in that species.

Sensilla of third palpal segment.—*Austroconops mcmillani* has sensilla scattered amongst ridges bearing spicules (Fig. 2B, C). This condition is similar to that in some species of *Leptoconops* (e.g. subgenera *Leptoconops s. str.*, *Proleptoconops* Clastrier). In other species of *Leptoconops* (e.g. subgenus *Holoconops* Kieffer), all Forcipomyiinae, and some Ceratopogoninae, the sensilla are grouped in a pit which is surrounded by short spicules. Other Ceratopogoninae and all Dasyheleinae have palpal sensilla in a group but not sunk into a pit, and individual sensillae are not separated by spiculate ridges.

If the shared similarities between *Austroconops* and some species of *Leptoconops* are homologous then the similarities between other *Leptoconops* and Forcipomyiinae plus some Ceratopogoninae would be convergent. It is equally likely that the similarity between *Austroconops* and some *Leptoconops* is convergent.

Vestigial empodium.—*Austroconops mcmillani* do, in contrast to the report of Wirth and Lee (1958), have empodia, although these are not as well developed as in most Forcipomyiinae. Outgroup comparisons show that Chironomidae have well developed empodia, while in Simuliidae and Thaumaleidae they are present but somewhat reduced. The relative development of the empodium is probably susceptible to homoplasy and a poor indicator of relationship.

Claw size.—Small equal claws are almost certainly a plesiomorphic feature, shared by

Leptoconops, *Austroconops*, Forcipomyiinae, Dasyheleinae, Culicoidini, many Ceratopogonini and many members of the Culicomorpha, including all Chironomidae.

Wing macrotrichia.—The presence or absence of macrotrichia appears highly susceptible to homoplasy. The absence of macrotrichia is characteristic of *Leptoconops*, *Austroconops*, and many Ceratopogoninae. Many Chironomidae, all Simuliidae, most Thaumaleidae and all Dixidae lack macrotrichia suggesting that the absence of macrotrichia within Ceratopogonidae is a plesiomorphic condition.

Remm (1975) suggested that the presence of macrotrichia was a synapomorphy of his Forcipomyiinae and his Ceratopogoninae. Macrotrichia are not present in many of the taxa included in Remm's Ceratopogoninae (e.g. *Serromyia* Meigen) making the character state suspect as a synapomorphy of these two subfamilies.

Wing venation.—The similarity between the wing venation of *Austroconops* and some "predaceous ceratopogonids" (Boorman and Lane, 1979) may be superficial. The direction of Rs and R_{2+3} of *Austroconops* is more angular and the tip of cell r_{4+5} is narrower. In addition, the relatively long costa, compared to *Leptoconops*, Forcipomyiinae and Dasyheleinae, may be plesiomorphic. Chironomidae, Thaumaleidae and Simuliidae all have relatively long costas (but see below).

Short costa.—On the basis of outgroup comparisons (see above under "Wing venation"), the short costa of Remm's Forcipomyiinae and Ceratopogoninae may be considered derived. However, it should be noted that, first of all, cells r_{2+3} and r_{4+5} are more slit-like in *Forcipomyia*, *Atrichopogon* and *Dasyhelea* than they are in Remm's Ceratopogoninae. The shape of these cells probably is correlated with the reduction of the length of the costa and the differences in their shape may suggest that they are not homologous. Secondly, several lineages of Chironomidae have a short costa (e.g. *Clu-*

nio Haliday, *Corynoneura* Winnertz) indicating, also, the possibility of homoplasy. Finally, if the shortened costa is taken as a derived character, it would also include *Leptoconops* and such a grouping would contradict a number of other synapomorphies (Fig. 8C). It seems likely that the shortened costa is in fact a plesiomorphic condition within the Ceratopogonidae and the longer costa of *Austroconops* and some Ceratopogoninae are reversals to the plesiomorphic state found in groups outside the Ceratopogonidae.

Medial vein branching distal to cross vein (r-m).—Remm (1975) uses this character as a synapomorphy of his Forcipomyiinae and Ceratopogoninae. However, a media branching distal to r-m cross vein is characteristic of many Nematocera, including all Culicoidea and Simuliidae. A media branching proximal to r-m is present in Thaumaleidae. Chironomidae lack M2, so that the character cannot be categorized in that family. This character state distribution makes the interpretation of the polarity difficult within Ceratopogonidae.

Pronotum fused with mesonotum.—We are unsure what, exactly, Remm (1975) was referring to when he discussed this character. We assume that he meant the relative development, medially, of the pronotum. If so, this character is not present in all the taxa Remm (1975) mentioned. A well developed pronotum is present in Stilobezziini. It is reduced medially in *Leptoconops*, *Austroconops*, Forcipomyiinae, Dasyheleinae, Culicoidini and Ceratopogonini. It is also reduced in Thaumaleidae, Simuliidae and some Chironomidae, but is well developed in some other Chironomidae. This suggests that the character is susceptible to homoplasy. Our phylogenetic conclusions imply that the well developed pronotum is secondarily derived in Stilobezziini, Sphaeromyiini, Heteromyiini, Stenoxenini and Palpomyiini.

Humeral pits.—These depressions on the anterolateral portion of the scutum are pres-

ent in *Leptoconops*, *Austroconops*, *Culicoides*, *Paradasyhelea* and *Neoculicoides* Boorman. The pits are also present but are less well developed in some other ceratopogonids. In some members of the Ceratopogoninae the humeral pits are indicated only by a bare patch in the midst of an otherwise pollinose scutum.

This character is poorly known and requires an intensive morphological study and survey of the distribution of the character state.

Male terminalia.—*Austroconops mcmillani* have unusual terminalia when compared to other ceratopogonids. However, some parts are similar to those of other Culicomorpha and especially to those of Simuliidae.

Wood and Borkent (1982), in comparing the male terminalia of various lineages within the Culicomorpha, concluded that the structures ventral to the parameres included two basic components: 1) the aedeagus, some with an aedeagal sclerite supporting the gonopore (called median sclerite in Simuliidae, aedeagus in Culicidae, aedeagal guide in Dixidae) and, 2) the ventral plate with a posterior, single median or pair of setose lobes (called aedeagus in Ceratopogonidae, ventral appendages in Thaumaleidae, dorsomedial lobes in Chironomidae, claspettes in Culicidae and prosopallus in Dixidae).

In many species of Culicomorpha, one or more of these parts may be absent or markedly modified, drawing into question the validity of whether these character states are actually the plesiomorphic condition within the Culicomorpha. Nevertheless, many of the early lineages within Culicomorpha families do share these characteristics.

We recognize these components in the male terminalia of *Austroconops mcmillani* and have labelled them as such in Fig. 4D, E, F, and G. In particular, the presence of an aedeagal sclerite which arises dorsally from the ventral plate, and which lies ventral to the opening of the gonopore is strik-

ingly similar to the condition found in the Simuliidae.

Although we recognize a distinct ventral plate and aedeagal sclerite in *A. mcmillani*, we are unsure of what exact homologies exist between this species and other ceratopogonids. The aedeagal sclerite recognized in *A. mcmillani* may be homologous only to the apex of the "aedeagus" recognized in other ceratopogonids, while the ventral plate is homologous to the lateral arms of the "aedeagus." Alternatively, Wood and Bor-kent (1982) considered the ventral plate of Simuliidae (and hence that of *A. mcmillani*) to be homologous to the entire "aedeagus" of Ceratopogonidae suggesting that the aedeagal sclerite present in *A. mcmillani* may have been lost in other ceratopogonids. This implies that the ventral plate of *A. mcmillani* is homologous to the entire "aedeagus" of other ceratopogonids.

One clue that suggests the aedeagal sclerite of *A. mcmillani* may be homologous to the apex of the "aedeagus" of other ceratopogonids is the presence of the ventrally directed point located subapically on the aedeagal sclerite (Fig. 4F). Many other male ceratopogonids have the tip of their aedeagus directed ventrally (e.g. at least some species in the following genera: *Atrichopogon*, *Culicoides*, *Isohelea* Keiffer, *Alluaudomyia* Kieffer, *Serromyia*, *Clinohelea* Kieffer, *Johannsenomyia* Malloch, *Sphaeromyia* Kieffer, *Palpomyia* Meigen). However, the aedeagal tip of many other ceratopogonids is directed posteriorly. In addition, we are uncertain if the condition is homologous in *Austroconops* and other Ceratopogonidae.

All species of Leptoconopinae in which the male terminalia have been adequately described, appear to lack all but the traces of any of these structures and possess either a simple rod shaped structure or only membranous cuticle ventral to the gonopore and between the gonocoxites. This is probably an autapomorphic loss of much of the ventral plate and aedeagal sclerite and provides no indication of the phylogenetic position

of *Leptoconops*. The ventral plate and aedeagal sclerite is also lost or reduced in some Dixidae, all Chaoboridae, and in most Chironomidae. We regard loss in each of these four families as independent.

Regardless of whether the aedeagal sclerite in *Austroconops* is homologous to the entire "aedeagus" of other ceratopogonids (except *Leptoconops*), or only to the apex of this structure, its complexity in *Austroconops* is consistent with our placement of it as the sister group of all other Ceratopogonidae other than *Leptoconops*. These other Ceratopogonidae would share the synapomorphy of the loss of the aedeagal sclerite or the loss of a strong distinction between a ventral plate and the aedeagal sclerite.

A. mcmillani has a single median setose lobe arising from the ventral plate. A single lobe is also present in Simuliidae, and some Thaumaleidae. A pair of lobes is present in Chironomidae, Dixidae and Culicidae. It is uncertain whether the single and paired conditions represent a homologous character. Even if they were, it would be difficult, at present, to interpret whether the single lobe of *Austroconops* was plesiomorphic or derived.

Some *Leptoconops* species appear to have a granulose area associated with the gonopore (called macule and accessory macules by Clastrier and Wirth, 1978) and this may be homologous to the setose lobe of *Austroconops*. Several other species of Ceratopogonidae (e.g. *Culicoides variipennis*, *C. sonorensis*) also have setose areas ventral to the "aedeagus." However, considering the placement of such species in the phylogeny of the Ceratopogonidae, it is doubtful whether the setose areas are homologous to the setose lobe possessed by *A. mcmillani*.

Shape of female abdominal sternite 9.— There may be more phylogenetic information in the shape of sternite 9 of Ceratopogonidae than noted above in character 12. Fig. 8B shows diagrammatically, the various configurations in shape of sternite 9 in representatives of the major lineages of Cer-

atopogonidae. In *Leptoconops* sternite 9 is a simple narrow band; in *Austroconops* sternite 9 forms a medial bend and has anteromedially projecting lateral apodemes; in Dasyheleinae (*Dasyhelea* Kieffer) sternite 9 often bears an anteromedial projection or forms a complete, anteromedial circular loop; in Forcipomyiinae (*Forcipomyia* Meigen and *Atrichopogon* Kieffer) sternite 9 forms a medial circular loop but with a posteromedial break; in Ceratopogoninae sternite 9 is a thick band with a medial separation.

In some species of Dasyheleinae and Forcipomyiinae the anterior portion of the loop is expanded anteriorly.

The similar, looplike condition of sternite 9 in Dasyheleinae and Forcipomyiinae may be a synapomorphy of those two taxa. We are uncertain which parts of the sternite 9 of *Austroconops* may be homologous to this loop; whether the lateral arms have joined medially to form an anterior closure or whether the lateral arms have been lost and the posterior bend has fused posteriorly to form the loop of Dasyheleinae and Forcipomyiinae.

The medial gap in sternite 9 of Ceratopogoninae and in the posterior portion of the circular loop of sternite 9 of Forcipomyiinae may be homologous and as a unique condition may be a synapomorphy of the two groups. However it is also possible that the complete anterior margin of the loop of Forcipomyiinae is homologous to sternite 9 of Ceratopogoninae, in which case there is no similarity. Hopefully, future morphological studies may be able to resolve the true homologies.

Spermathecal number.—Two large and one small spermathecae are found in a number in lineages of Ceratopogonidae, including *Leptoconops*, Culicoidini, Ceratopogonini, Stilobezziini, Sphaeromiini, Heteromyiini, and Palpomyiini. This alone makes the presence of two large and one small spermathecae in *Austroconops* difficult to inter-

pret. In addition, other families of Culicomorpha have from one to three spermathecae, making outgroup comparisons difficult to apply. Chironomidae have 2–3, Simuliidae have 1 (but 3 ducts present), Dixidae have 1, Chaoboridae have 1 (*Coretrella* Coquillett) or 3, and Culicidae have 1–3.

CONCLUSION

Our analysis of character states supports the hypothesis that *Austroconops* is the sister group of Forcipomyiinae plus Dasyheleinae plus Ceratopogoninae. The sister group of this entire assemblage is Leptoconopinae (Fig. 8C). Alternatively, three character states, the shape of the antennal pedicel, the shape of the 13th flagellomere, and the four-segmented maxillary palpus, all of which exhibit some homoplasy, suggest that *Austroconops* could be the sister group of *Leptoconops*. The question can be tested by the discovery of further character states of the adults and particularly those of the presently unknown larva and pupa of *Austroconops memmillani*.

It seems clear that the hypothesis that *Austroconops* is closely related to *Culicoides* (Wirth and Lee, 1958) or any other member of the Ceratopogoninae (Boorman and Lane, 1979) is not supported by our investigation.

Our results bring into question the subfamilial status of *Austroconops*. Our conclusion concerning the placement of *Austroconops* (Fig. 8C) indicates that the genus should be given its own new subfamily, named Austroconopinae. However, if further investigations support the hypothesis that the genus is the sister group of *Leptoconops*, *Austroconops* might be considered as a member of Leptoconopinae.

Our conclusions can be used to address the question of the plesiotypic feeding habits of the Ceratopogonidae. The presence of biting mouthparts in many lineages of Culicomorpha includes many Ceratopogonidae (including the basal lineages), some Chiro-

nomidae, Simuliidae, Chaoboridae (*Corethrella*), and Culicidae. This strongly suggests that this condition is plesiomorphic to the Ceratopogonidae (Downes, 1958).

The presence of vertebrate blood feeding in *Leptoconops*, *Austroconops*, some Forcipomyiinae and some Ceratopogoninae (*Culicoides*), strongly suggests that this condition is plesiotypic to the family. Consequently, the many ceratopogonids which feed on other insects (also the loss of any biting habit at all) must be considered as exhibiting the derived condition within the Ceratopogonidae.

ACKNOWLEDGMENTS

We are grateful to Leo Forster for his skillful preparation of the specimens on microscope slides and the resultant photographs. The masterful execution of the line drawings was completed by Barry Flahey. His commitment to accurate illustration added significantly to our study.

We acknowledge the Director of the Western Australian State Department of Conservation and Land Management for permission to make the collections in Yanchep National Park and the resident Head Ranger, Ron Chandler and his staff for their courteous response. We thank also T. J. Ridsdill Smith, CSIRO, Division of Entomology, Floreat Park, Western Australia for his help with bookings, loan of equipment and advice leading to collection of the previously unknown males of *A. mcmillani*. The project was supported in part by Grant No. 8530 from the Rural Credits Development Fund, Australia.

We also thank the following for suggestions and helpful criticisms of our manuscript: Douglas C. Curry, J. Antony Downes, Gary Gibson, Bill Grogan, and Monty Wood. We are particularly grateful to Monty Wood for the hours spent discussing the characters presented in this paper, especially the homologies of the male genitalia within the Culicomorpha.

LITERATURE CITED

- Boorman, J. and R. P. Lane. 1979. A new genus and species of Ceratopogonidae (Diptera) closely related to *Culicoides* from West Africa. *J. Nat. Hist.* 13: 327-332.
- Clastrier, J. 1971. Isolement et description de la larve de *Leptoconops* (*Leptoconops*) *irritans* Noé, 1905 (Diptera, Ceratopogonidae). *Ann. Parasitol. Hum. Comp.* 46: 737-748.
- Clastrier, J. and W. W. Wirth. 1978. The *Leptoconops kerteszi* complex in North America (Diptera: Ceratopogonidae). *U.S. Dep. Agric. Tech. Bull. No.* 1573. 58 pp.
- Downes, J. A. 1958. The feeding habits of biting flies and their significance in classification. *Ann. Rev. Entomol.* 3: 249-266.
- Downes, J. A. and W. W. Wirth. 1981. Ceratopogonidae [chapter] 27, pp. 393-421. *In* McAlpine, J. F. et al., eds., *Manual of Nearctic Diptera*. Vol. 1. Res. Branch Agric. Can. Ottawa. Mono. 27, 674 pp.
- Gad, A. M. 1951. The head-capsule and mouth-parts in the Ceratopogonidae (Diptera-Nematocera). *Bull. Soc. Fouad I. Entomol.* 35: 17-75.
- Harbach, R. E. and K. L. Knight. 1980. Taxonomist's glossary of mosquito anatomy. Plexus Publishing, Marlton, New Jersey, 415 pp.
- Hennig, W. 1973. Diptera (Zweiflügler). *In* Handbuch der Zoologie. 2. Aufl., Bd. 4, Hfte 2, T. 3/31 Lf. 20. 337 pp.
- Krivoshaina, N. P. 1962. Pre-imaginal stages of *Leptoconops* (*Holoconops*) *borealis* Gutz. and the systematic position of the *Leptoconops* group (Diptera, Nematocera) (in Russian). *Zool. Zh.* 41: 247-251.
- Lawson, J. W. H. 1951. The anatomy and morphology of the early stages of *Culicoides nubeculosus* Meigen (Diptera: Ceratopogonidae = Heleidae). *Trans. R. Entomol. Soc. Lond.* 102: 511-570, pl. 1.
- Nielsen, A. 1951. Contributions of the metamorphosis and biology of the genus *Atrichopogon* Kieffer (Diptera, Ceratopogonidae) with remarks on the evolution and taxonomy of the genus. *Det Kongelige Danske Videnskabernes Selskab. Biologiske Skrifter* 6(6): 95 pp., 2 pls.
- Remm, H. 1975. On the classification of the biting midges (Diptera, Ceratopogonidae) (in Russian). *Parasitologiya* 9: 393-397.
- Saether, O. A. 1977. Female genitalia in Chironomidae and other Nematocera: Morphology, phylogenies, keys. *Bull. Fish. Res. Board Can.* 197. 209 pp.
- Saunders, L. G. 1924. On the life history and the anatomy of the early stages of *Forcipomyia* (Dip-

- tera, Nemat., Ceratopogoninae). Parasitology 16: 164-213, pls. 10-12.
- Wenk, P. 1962. Anatomie des Kopfes von *Wilhelmia equina* L. (Simuliidae syn. Melusinidae, Diptera). Zool. Jahrb. Anat. 80: 81-134.
- Wiley, E. O. 1981. Phylogenetics: The theory and practice of phylogenetic systematics. Wiley, Toronto. xv + 439 p.
- Wirth, W. W. and D. J. Lee. 1958. Australasian Ceratopogonidae (Diptera, Nematocera). Part VIII: A new genus from Western Australia attacking man. Proc. Linn. Soc. N.S.W. 83: 337-339.
- Wirth, W. W. and S. Navai. 1978. Terminology of some antennal sensory organs of *Culicoides* biting midges (Diptera: Ceratopogonidae). J. Med. Entomol. 15: 43-49.
- Wirth, W. W., N. C. Ratanaworabhan, and F. S. Blanton. 1974. Synopsis of the genera of Ceratopogonidae (Diptera). Ann. Parasitol. (Paris) 49: 595-613.
- Wood, D. M. and A. Borkent. 1982. Description of the female of *Parasimulium crosskeyi* Peterson (Diptera: Simuliidae), and a discussion of the phylogenetic position of the genus. Mem. Entomol. Soc. Wash. 10: 193-210.
- Wood, D. M. and A. Borkent. (In press). Phylogeny and classification of the Nematocera. Ch. 114. Manual of Nearctic Diptera. Vol. 3. Res. Branch Agric. Can. Ottawa.
- Zilahi-Sebess, G. 1960. Über die Systematische Stellung der *Leptoconops*-gruppe (Diptera, Nematocera). Acta Zool. 6: 227-235.